# POLAROTAXIS IN COPEPODS. II. THE ULTRASTRUCTURAL BASIS AND ECOLOGICAL SIGNIFICANCE OF POLARIZED LIGHT SENSITIVITY IN COPEPODS

#### BRUCE L. UMMINGER

#### Bingham Laboratory, Yale University, New Haven, Conn. 06520

The ability to perceive linearly polarized light and to determine its plane of polarization has been demonstrated both behaviorally and electrophysiologically in a great number of species, mostly in arthropods but also in cephalopod mollusks (Waterman, 1966a). The mechanism of polarized light perception is localized at the retinal level and, in the cases adequately known, apparently depends on a two-channel system comprising a pair of dichroic analyzers oriented at right angles (Waterman, 1966b; Waterman and Horch, 1966; Eguchi and Waterman, 1966, 1967).

In a previous paper (Unminger, 1968), polarotaxis was behaviorally demonstrated in the copepod *Cyclops vernalis*. This was the first reported case of polarized light sensitivity in an organism possessing a naupliar eye exclusively. Earlier investigators (Stockhammer, 1959; Jander, 1966) had failed to find polarotaxis in copepods.

The purposes of this paper, then, are two-fold: First, an ultrastructural examination of the naupliar eye of *Cyclops vernalis* was undertaken to determine if there was a two-channel system of microvilli present as in polarotactic arthropods with compound eyes. Secondly, a great number of copepod species were examined for polarotactic behavior to see if the ability to perceive polarized light is universal or limited to only a few species of copepods. If polarotaxis is not universally present in copepods, this would explain the failure of Stockhammer and Jander to find it in the species they studied.

# FINE STRUCTURE OF THE NAUPLIAR EYE

### Methods

To determine whether the polarotactic behavior of *Cyclops vernalis* Fischer could be explained by some structural component of the naupliar eye, the fine structure of the eye was examined. The entire copepod was first fixed for two hours with 5% glutaraldehyde buffered in 0.1 M Sorenson's phosphate solution at pH 7.4 (Sabatini, Bensch and Barrnett, 1963). After washing with buffer, the copepods were cut in half and the metasomes post-fixed for another two hours in 2.5% osmium tetroxide, also buffered at pH 7.4 with Sorenson's solution. Fixation was followed by acetone dehydration, transfer to propylene oxide and embedding in epoxy resin (Luft, 1961). Sections were cut with a Porter-Blum MT-2 microtome and stained with uranyl acetate and lead citrate (Reynolds, 1963). Observations were then made in a Philips 200 electron microscope.

#### STRUCTURAL BASIS FOR POLAROTAXIS



FIGURE 1. Longitudinal section through a dorsal ocellus of *Cyclops vernalis*. A. Portions of the other dorsal ocellus, DO, and the single ventral ocellus, VO, can be seen at the bottom. The two dorsal ocelli and the ventral ocellus make up the tripartite naupliar eye. con = conjunctiva, er = endoplasmic reticulum, gly = glycogen granules, gol = Golgi complex, m = mitochondrion, n = nucleus, pha = phaosome, pig = pigment cell, ra = retinular cell axons, RC = retinular cell, rh = rhabdom, tap = tapetum, vac = vacuole. Box represents area enlarged in B. B. Higher-power detail of the rhabdom.

# Results

The "eye" of *Cyclops vernalis*, as is typical of most copepods, is composed of three ocelli on the anterodorsal region of the protocerebrum. The two dorsal ocelli each measure about 25  $\mu$  in diameter and point in a lateral direction. The single ventral ocellus points ventrally towards the rostrum.

The dorsal ocellus (Fig. 1) is composed primarily of several retinular cells whose inner ends have projections of microvilli forming the light-sensitive rhabdom. Of particular interest is the arrangement of these microvilli: those of one retinular cell meet those of another retinular cell at right angles (Fig. 1B). The retinular cells contain phasomes, much endoplasmic reticulum and many glycogen particles. A reflecting tapetum forms a hemispherical cup around the bases of the light-sensitive retinular cells whereas a thin conjunctiva covers their distal surfaces. Surrounding the tapetum, which is tightly packed with crystals, is a screening pigment cell containing granules of melanin.

Light enters the ocellus through the conjunctiva and passes through the distal parts of the retinular cells. It then strikes the rhabdom which has its microvilli perpendicular to the incoming light.

# POLAROTACTIC BEHAVIOR IN COPEPODS

# Material and Methods

In an attempt to discover whether polarotaxis is widespread in copepods, a number of species from several orders of the Subclass Copepoda were examined. Several of the species studied had simple naupliar eyes as does *Cyclops vernalis*, whereas others had elaborately modified naupliar eyes, often with cuticular lenses and movable parts (Vaissière, 1961).

In experiments performed at the Duke University Marine Laboratory, the copepods were freshly captured each day and examined at times of natural sunrise, midday and sunset; none were cultured nor kept on a 12-hour light, 12-hour dark cycle as was *Cyclops vernalis* (Unminger, 1968). At Yale University, specimens of *Tisbe furcata* (Baird) were cultured and kept on a 12-hour light, 12-hour dark cycle of illumination. In addition, the fresh-water *Diaptomus shoshone* Forbes was studied after it had been flown to New Haven from Colorado.

All species were tested with linearly polarized light in experiments identical to those performed on *Cyclops vernalis* in a previous paper (Umminger, 1968).

#### Results

Polarotactic behavior like that of *Cyclops vernalis* could not be elicited in all the species studied. Several species oriented to polarized light whereas other species showed no polarotactic responses whatsoever. Using linearly polarized light from above, *Caligus rapax* Milne Edwards, *Centropages hamatus* (Lilljeborg) and *Diaptomus shoshone* Forbes all swam at right angles to the plane of polarization. *Pontella meadii* Wheeler and *Tisbe furcata* (Baird) both oriented  $0^{\circ}$ ,  $\pm 45^{\circ}$ and  $90^{\circ}$  (4 peaks) to the plane of polarization. *Labidocera aestiva* Wheeler oriented  $0^{\circ}$  to the plane of polarization. In all these species, however, the angle of orientation was the same at all times of day and under all conditions of illumination. There were no rhythms in polarotaxis.

The species showing no polarotactic responses were *Pseudodiaptomus coronatus* Williams, *Acartia tonsa* Dana, *Eucalanus monachus* Giesbrecht, *Corycaeus speciosus* Dana, *Oncaea venusta* Philippi, *Oithona similis* Claus, *Oithona nana* Giesbrecht, *Oithona spinirostris* Claus and *Euterpina acutifrons* (Dana).

#### Discussion

# Polarized light perception and eye structure

In many arthropods, particularly Crustacea, and cephalopod mollusks, where polarized light perception has been best demonstrated, there is always a regular arrangement of two sets of retinal microvilli which comprise the rhabdom, one set being perpendicular to the other (Eguchi and Waterman, 1966; Waterman, 1966c). If the dichroic molecules of visual pigment are oriented so that their major axis of absorbance is parallel to the long axis of the microvilli, then the orthogonal arrangement of microvilli functions as a two-channel retinal analyzer of polarized light (Waterman, 1966b; Waterman and Horch, 1966; Eguchi and and Waterman, 1967). Thus the set of retinular cells with the long axes of their microvilli parallel to the plane of polarization will be maximally stimulated by the incoming polarized light, whereas the remaining retinular cells with microvilli having their long axes perpendicular to the plane of polarization will be minimally stimulated. If both sets of microvilli are at a 45° angle to the plane of polarization, then both will be stimulated to the same degree. If the organism compares the stimulation in one set of microvilli to the stimulation in the other set, it has instantaneous information as to its orientation with respect to the plane of polarization.

However, if an organism has only one set of parallel microvilli, it might also orient to polarized light, but it could not get an instantaneous bearing. In this case, the organism would have to compare the stimulation received by this one set of parallel microvilli at one point in time with the stimulation received at another point in time. Thus, if the organism were oriented so that the long axes of the microvilli were parallel to the plane of polarization, the retinal stimulation would be maximal. Then, if the organism tilted or turned a bit, the microvilli would no longer be parallel to the plane of polarization, thus reducing retinal stimulation. The comparison of successive stimulations in time would allow the organism to orient so that retinal stimulation was maximal; in this way the microvilli would always be parallel to the plane of polarization. However, a very real disadvantage to this system is that changing light intensities might not be discriminated from the *c*-vector responses. A decrease in light intensity might confuse the organism if it interpreted such a change as a deviation from its position of orientation to the plane of polarization. One would expect, then, that such a one-channel system is not ideally suited for polarotactic behavior.

The fine structure of the eye of *Cyclops vernalis* clearly shows regions of mutually perpendicular microvilli, suggesting that this geometric arrangement is responsible for the copepod's perception of polarized light. Furthermore, both sets of microvilli are perpendicular to the incoming light as is typically the case

of compound or camera eyes sensitive to polarized light. When the copepod is swimming in either of its usual positions (horizontally or vertically), the laterally pointing dorsal ocelli (Fig. 1) will be oriented so that one set of microvilli is parallel to the naturally horizontal plane of polarization whereas the other set is perpendicular to this plane. Therefore, the vertical and horizontal directions of the microvilli correspond to the vertical and horizontal axes of the copepod's normal spatial orientation, a situation closely similar to that in decapod crustaceau compound eyes (Waterman and Horch, 1966; Eguchi and Waterman, 1967) and in cephalopod camera eyes (Tasaki and Karita, 1966).

Unfortunately, no electron micrographs are available for the other species of copepods studied, but light microscopy by Vaissière (1961) suggests that *Centropages typicus* has parallel rows of microvilli in its naupliar eye whereas *Corycacus clausi* has no regular arrangement of microvilli, the entire rhabdom being curved so that the microvilli are not parallel. In the experimental studies presented here, *Centropages hamatus* is polarotactic whereas *Corycacus speciosus* is not. This additional information suggests that polarotactic behavior is correlated with a

Species	Polaro- tactic	Medium	Habitat	Vertical migration	Food habits	Eye structure
Calanoida						
Labidocera aestiva	Yes	SW	Pelagic*	Yes††	Omnivore <sup>(a (a</sup>	Complex
Pontella meadii	Yes	SW	Pelagie*	_	Omnivore+	Complex
Centropages hamatus	Yes	SW	Pelagic*	$Yes^{\phi}$	Omnivore <sup>@@@</sup>	Complex
Diaptomus shoshone	Yes	FW"	Pelagic**	$Yes^{\phi\phi}$	Predator**	Simple
Pseudodiaptomus coronatus	No	SW.	Pelagic*	Yes <sup>#</sup>	Probably herbiyore	Simple
Acartia tonsa	No	SW	Pelagic*	Yes##	Omnivore@@	Simple
Eucalanus monachus	No	SW	Pelagic*		Probably herbivore	Simple
Cyclopoida						
Cyclops vernalis	Yes	FW	: Littoral†		Predator <sup>++</sup>	Simple
Corycaeus speciosus	No	SW	Pelagic*	Yesé	Predator <sup>+</sup>	Complex
Oncaea venusta	No	SW	Pelagic*		Probably herbivore	Simple
Oithona similis	No	SW	Littoral*	Yescé	Predator <sup>\$</sup>	Simple
Oithona nana	No	SW	Pelagic*	$Yes^{\phi}$	Herbivore <sup>\$\$</sup>	Simple
Oithona spinirostris	No	SW	Pelagic*	Yes@	Predator*	Simple
Harpacticoida			0			1
Tisbe furcata	Yes	SW	Littoral*		Herbivore <sup>=</sup>	Simple
Euterpina acutifrons	No	SW	Pelagic*		Scavenger ::	Simple
Caligoida						1
Caligus rabax	Yes	SW.	Pelagic*		Exoparasite*	Complex

		TABLE	ł		
Relation	of	polarotaxis	to	copepod	ecology

' Sea water; " fresh water.

\*Wilson, 1932; \*\*Brooks, J. L., personal communication; †Pennak, 1966; ††Parker, 1902; <sup>6</sup>Hansen, 1951; <sup>¢¢</sup>Pennak, 1944; <sup>#</sup>Grice, 1957; <sup>##</sup>Schallek, 1942; <sup>¢</sup>Roehr and Moore, 1965; <sup>§¢</sup>Bogorov, 1946; <sup>@</sup>Moore and O'Berry, 1957; <sup>@</sup>@Anraku and Omori, 1963; <sup>+</sup>Personal observation; <sup>++</sup>Dziuban, 1964; <sup>\$</sup>Marshall and Orr, 1966; <sup>\$\$</sup>Murphy, 1923; <sup>=</sup>Battaglia and Bryan, 1964; <sup>::</sup>Lebour, 1923. geometrically regular arrangement of microvilli within the eye, a condition essential to the dichroic rhabdom analyzer mechanism.

Of the copepods studied, five had very elaborate naupliar eyes with cuticular lenses and often with movable parts (Table I). Of these five species with such complex eyes, four gave evidence of perceiving polarized light. Of the eleven species with simple naupliar eyes, only three responded specifically to polarized light. Since polarized light can be perceived by both simple and complex naupliar eyes and since its perception clearly does not depend on lenses or other gross structural modifications, then this again points to the ultrastructure of the eye as the site of polarized light perception. Actually, the tendency for polarized light perception to be more prevalent in forms with complex eyes may be explained by the fact that all these species are predators (Table I).

# Polarized light perception by copepods

Although polarized light sensitivity has been reported for cephalopod mollusks with camera eyes (Moody and Parriss, 1960, 1961; Jander, Daumer and Waterman, 1963; Tasaki and Karita, 1966), for arthropods with compound eyes (Baylor and Smith, 1953; Jander and Waterman, 1960; Waterman, 1966a) and for insect larvae (Wellington, 1953, 1955; Waterman, 1966a), mites (Baylor and Smith, 1953) and spiders (Papi, 1955; Waterman, 1966a) with simple ocelli, it has only once been reported for an organism with a naupliar eye exclusively (Umminger, 1968). However, since Stockhammer (1959) was unable to find polarotaxis in copepods of the *Cyclops* group and since Jander (1966) could not demonstrate polarized light sensitivity in the copepods *Macrocyclops albidus, Cyclops strenuus* and *Labidocera* spp., it appeared that at least some copepods did not exhibit polarotaxis. The present paper confirms definitely that the naupliar eye can perceive polarized light, but that this ability is not to be found universally in copepods.

The failure of Stockhammer and Jander to find polarotaxis in copepods could be due either to organismal or to experimental factors. In the former case, the species investigated actually may not have been able to perceive polarized light. Since the structure of the naupliar eye varies so greatly with the Crustacea as a whole (Elofsson, 1963) and even within the Copepoda (Vaissière, 1961), it is entirely possible that the species examined by Stockhammer and Jander did not possess eyes with the regular two-channel arrangement of microvilli necessary for polarized light perception. This appears to be the reason why *Corycacus speciosus* showed no polarotaxis in the present paper.

For example, Fahrenbach (1964) has made an ultrastructural study of the eye of *Macrocyclops albidus*. The eye contains great masses of microvilli running parallel, but not perpendicular, to one another in a tightly packed array. As previously discussed, such a one-channel system is not ideally suited for polarized light detection and, indeed, Jander (1966) observed no polarotaxis in this species.

Moreover, even if a species did possess the appropriate eye structure and did perceive polarized light, it is entirely possible that the copepods did not behaviorally react to it because they do not use polarized light as a sensory cue in their orientation behavior; *i.e.*, they perceive, but ignore, polarized light. In addition to such organismal factors, several experimental factors might also explain the failure of Stockhammer and Jander to observe polarotaxis in copepods. Thus the time of observation may have been wrong. That is, there may have been a rhythm in polarotaxis such that observations were made only during the unoriented phase of behavior. This explanation seems likely for those copepods of the *Cyclops* group. If other members of the genus *Cyclops* show a rhythm as does *Cyclops vernalis* (Umminger, 1968), then orientation peaks would appear at dusk, midday and dawn, the times when most investigators are least likely to be observing copepods. At other times, the copepods would be in a transitional state and appear unoriented.

Another experimental factor which may explain the failure to obtain polarotactic responses is as follows: The copepods may have sensed the polarized light, but the correct combination of illumination parameters (absolute intensity, wave-length, angular distribution of intensity, changing intensity, etc.) was not employed to release the corresponding polarotactic behavior.

# Ecological significance of polarotaxis

In a previous paper, a polarotactic rhythm in Cyclops vernalis occurred in an ecologically meaningful way, implicating it as a behavioral mechanism in vertical migration (Umminger, 1968). In the present paper, however, all the copepods with polarotactic behavior showed no rhythm in their responses. This may be due either to the absolute lack of such rhythms or to the failure of the experiments to provide the correct combination of illumination (or other) parameters needed to release the rhythm. In the experiments with Cyclops vernalis, for example, the rhythm was released only in the presence of a uniform angular distribution of light intensity. If such an esoteric cue is needed as a prerequisite for the rhythm in this case, then equally unsuspected conditions may be necessary to release the rhythms in the other copepods with polarotactic behavior.

Moreover, as discussed above, the lack of demonstrated polarotaxis in other species of copepods examined in this paper does not necessarily mean that the copepods in question cannot perceive linearly polarized light, but may indicate the failure of the experimental conditions to elicit a response to it. On present evidence, however, one must assume that orientation rhythms are not present in some copepods with polarotaxis and that other copepods do not have polarotactic behavior.

If one accepts the observed differences in polarotaxis as real, then some clue as to their ecological significance might come from comparing the ecologies of polarotactic and non-polarotactic species (Table 1).

Obviously polarotaxis has no relation to habitat since it is found in both salt-water and fresh-water forms and is common in both pelagic and littoral copepods. Furthermore, natural vertical migrations have been reported in forms without polarotaxis as well as in forms with polarotaxis. Therefore, although polarotaxis may be useful for orientation in vertical migration as with *Cyclops vernalis*, polarized light sensitivity may not be necessary for such migrators.

One rather striking similarity among polarotactic copepods is their tendency to be either predatory or omnivorous. Of the seven copepods showing polarized light sensitivity, six are either predators or onnivores. This suggests that the ability to perceive polarized light might be of greater advantage to a copepod with predatory habits than to one that is strictly herbivorous. This may be related to the findings of Lythgoe and Hennmings (1967) who reported that polarized light sensitivity in clear waters enables distant objects to be more clearly seen and causes contrasts in intensity to be much sharper. Such an improvement in visual ability would seem to be more advantageous to a predator than to an herbivore. One might expect, then, the findings that polarized light sensitivity is most common in predators.

The improved visual ability imparted to predators by polarized light sensitivity does not preclude, however, the additional use of this sensitivity for spatial orientation and migration. The very fact that the predators actively orient to the plane of polarization demonstrates that they do more than passively perceive it; they use it to modify their spatial orientation as well.

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# SUMMARY

1. The ability of *Cyclops vernalis* to perceive polarized light has an ultrastructural basis in the presence of mutually perpendicular microvilli in its naupliar eye.

2. Laboratory investigations with several species of copepods were conducted to determine the extent of polarized light sensitivity in this group. Polarotaxis was not found to be universally present in copepods, but apparently depended on the presence of mutually perpendicular microvilli in the rhabdom of the naupliar eye.

3. Polarotaxis showed no correlation with the presence of a complex, rather than simple, naupliar eye.

4. The ability to perceive polarized light was more prominent in predatory than in herbivorous species, suggesting that its function might be to enable the copepods to discern distant objects more clearly, in addition to its role in orientation during vertical migration.

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